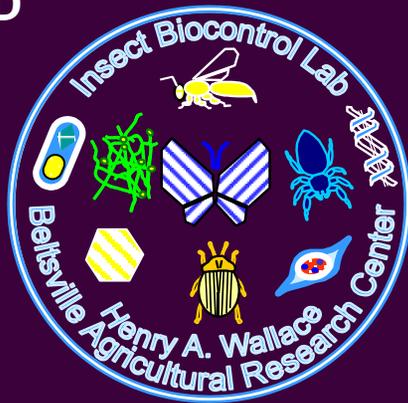


Ectoparasitoid carabids and their beetle hosts

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Insect parasitoids

A **parasitoid** is an organism which develops on or in another single (“host”) organism, extracts nourishment from it, and kills it as a direct or indirect result of that development (following Kuris 1974)

Found in the 3 major holometabolous orders:

Hymenoptera: 56 families

Diptera: 22 families

Coleoptera: 11 families

Parasitoid Beetles

Coleopteran families involved: eleven, including Stylopidae, Meloidae, Rhipiphoridae, Rhipiceridae, Cleridae, Scarabeidae, Staphylidae, and **Carabidae**

Coleoptera attack only arthropod hosts, of 8 orders:
Coleoptera (6 families), Hymenoptera (4), and one family each in the Lepidoptera, Diptera, Thysanoptera, Blattaria, Thysanura, and Diplopoda

Host searching is almost always by the first-instar beetle larva;
some are phoretic

Parasitoid Beetles

Habitat of beetle hosts

dead wood (ancestral for the majority of clades)

substrate zone

green plants

Trophic transitions

predatory → parasitoid

herbivore → parasitoid

Great interest in the evolution of these transitions

Aleochara (Staphylinidae) and *Lebia* are parasitoids of important pests

Carabid Trophic Diversity

Caribidae is an ancient group and is highly speciose

Not surprising that they display diversity in form and ecology

Stereotype: “ground” beetles which are generalist predators

Erwin has destroyed the “ground” part

We should finish off the “generalist” generalization !

Many examples of specialization:

Challenge posed by Erwin (1971)

is to discover ecology and to map

evolutionary transitions in feeding habits

Carabids as parasitoids

Still a novel concept; carabids are stereotyped as “generalist predators” even by entomologists who should know better

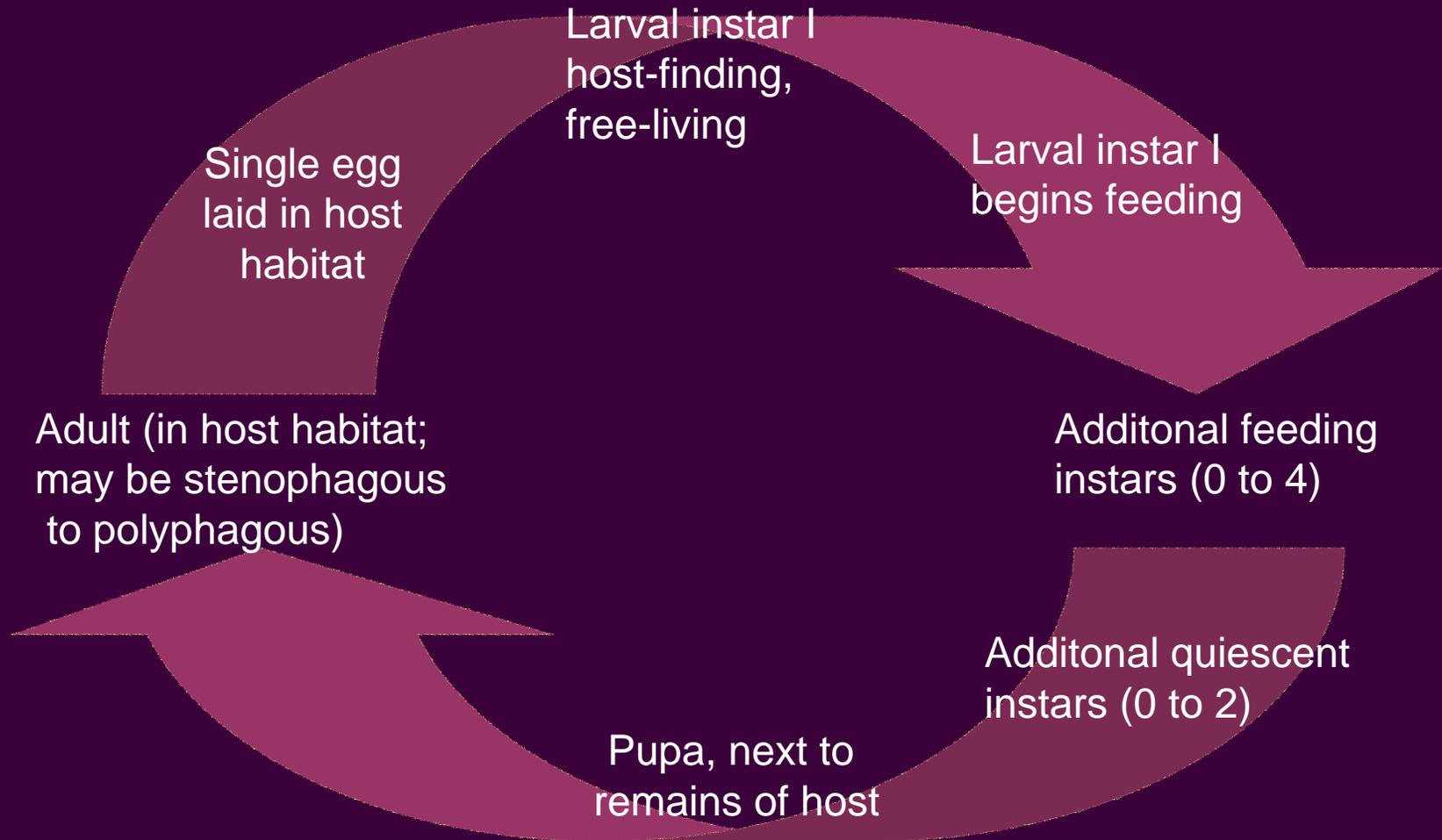
3 tribes known to be parasitoid

Brachinini water beetle pupae; carabid pupae

Peleciini young millipeds; chrysomelid pupae

Lebiini chrysomelid pupae

Carabid parasitoids: Basic life history



Brachinus



Eisner, numerous publications

Brachinus

COVER

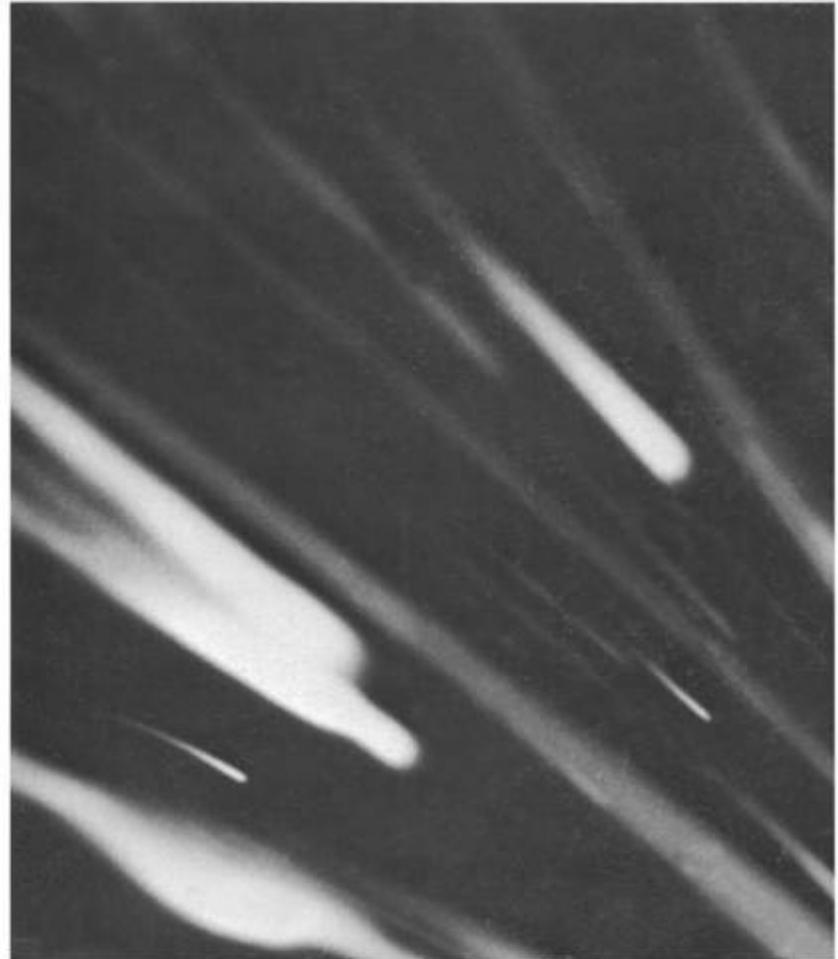
Droplets ($\times 250$) of the defensive spray of a bombardier beetle on their way to an enemy target. The spray is generated in an exergonic set of chemical events, and is ejected at 100°C . Predators are instantly repelled. See page 61. [D. Aneshansley and T. Eisner, Cornell University]

Aneshansley, D.J., T. Eisner, J.M. Widom, B. Widom. 1969. Biochemistry at 100 degrees C: Explosive Secretory Discharge of Bombardier Beetles (*Brachinus*) Science 165: 61-63.

SCIENCE

4 July 1969
Vol. 165, No. 3888

AMERICAN ASSOCIATION FOR THE ADVANCEMENT OF SCIENCE

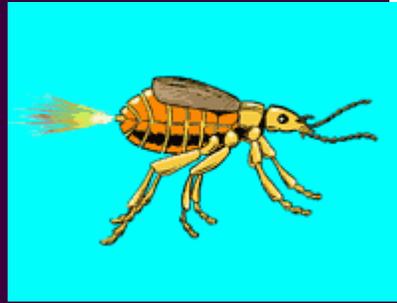
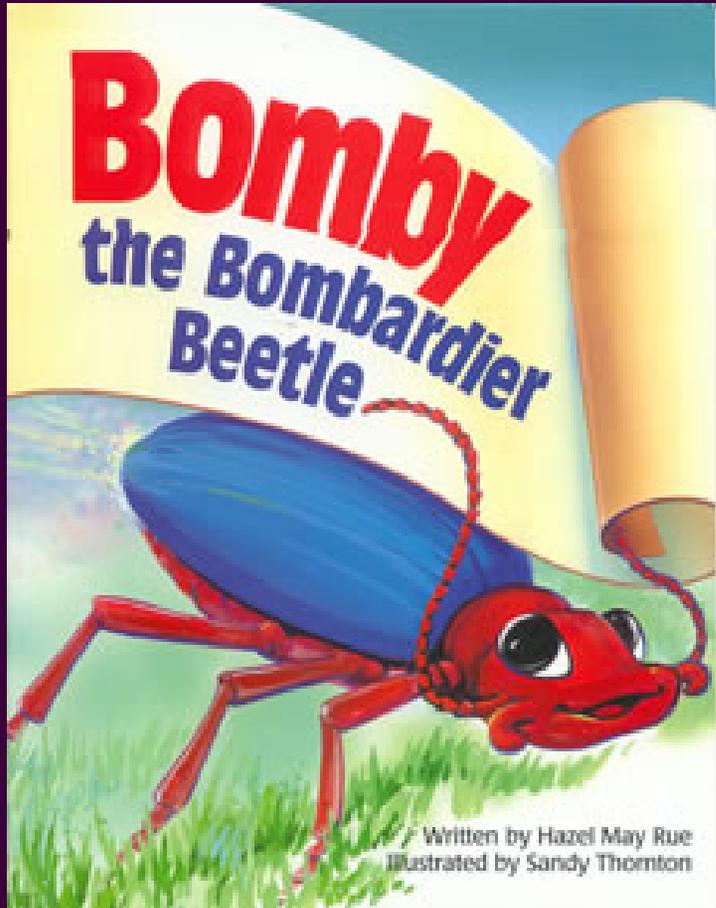


Brachinus

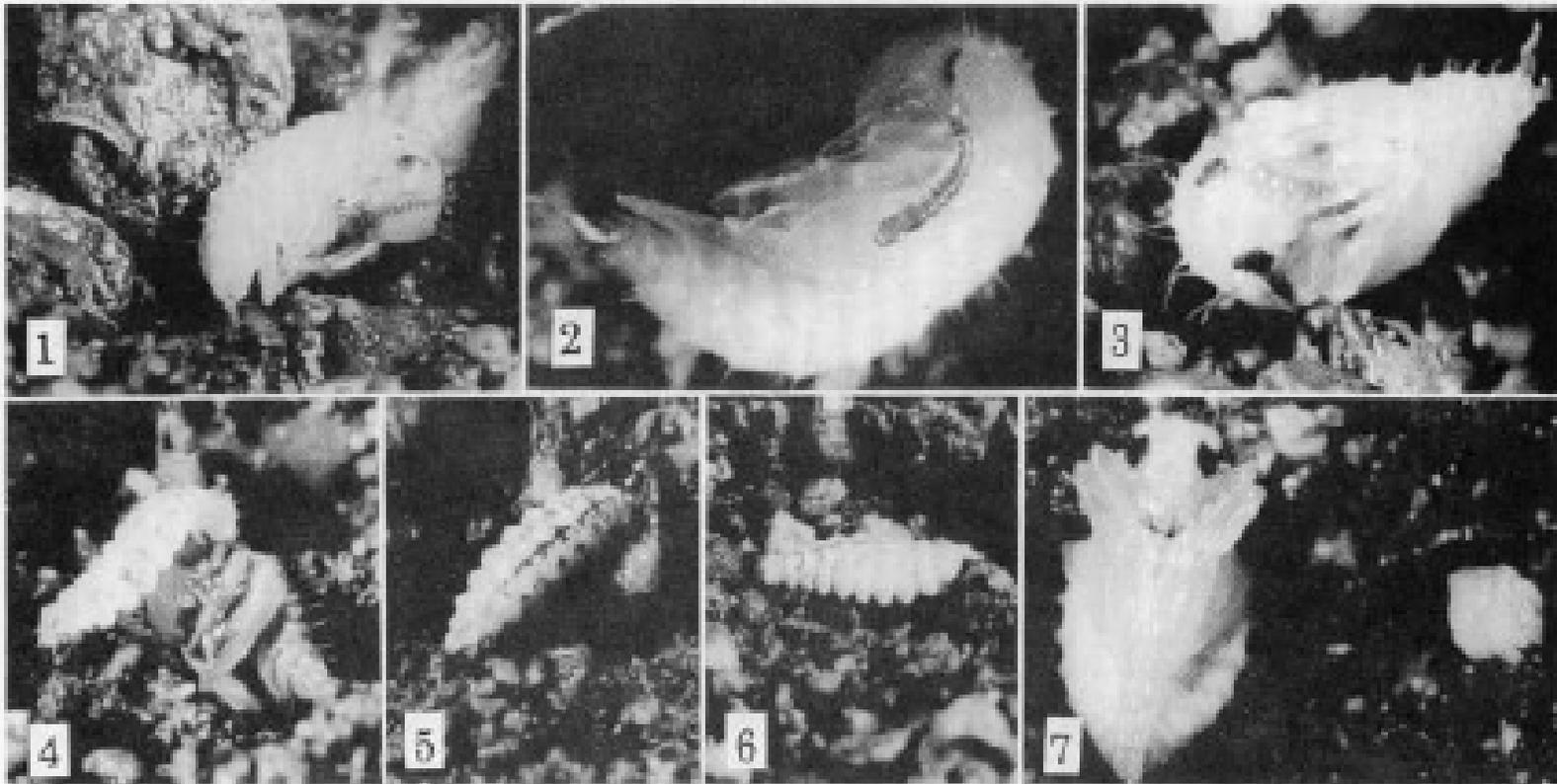


US Postal Service, 1999

Brachinus



Brachinus pallidus



PHOTOGRAPH 1. Two first instar *Brachinus pallidus* larvae with the pupa of *Tropisternus ellipticus* in the pupal chamber of the latter. PHOTOGRAPH 2. First instar of *B. pallidus* on pupa of *T. ellipticus*. PHOTOGRAPH 3. Second instar of *B. pallidus* on pupa of *T. ellipticus*. PHOTOGRAPH 4. Third instar *B. pallidus* on pupa of *T. ellipticus*. PHOTOGRAPH 5. Fourth instar of *B. pallidus* with remains of pupa of *T. ellipticus*. PHOTOGRAPH 6. Fifth instar of *B. pallidus* in pupal chamber of *T. ellipticus* after the latter was consumed. PHOTOGRAPH 7. Pupa of *B. pallidus* in pupal chamber of *T. ellipticus*.

Saska P, Honek A. 2004. Development of the beetle parasitoids, *Brachinus explodens* and *B. crepitans* (Coleoptera: Carabidae). *Journal of Zoology London* 262: 29-36.

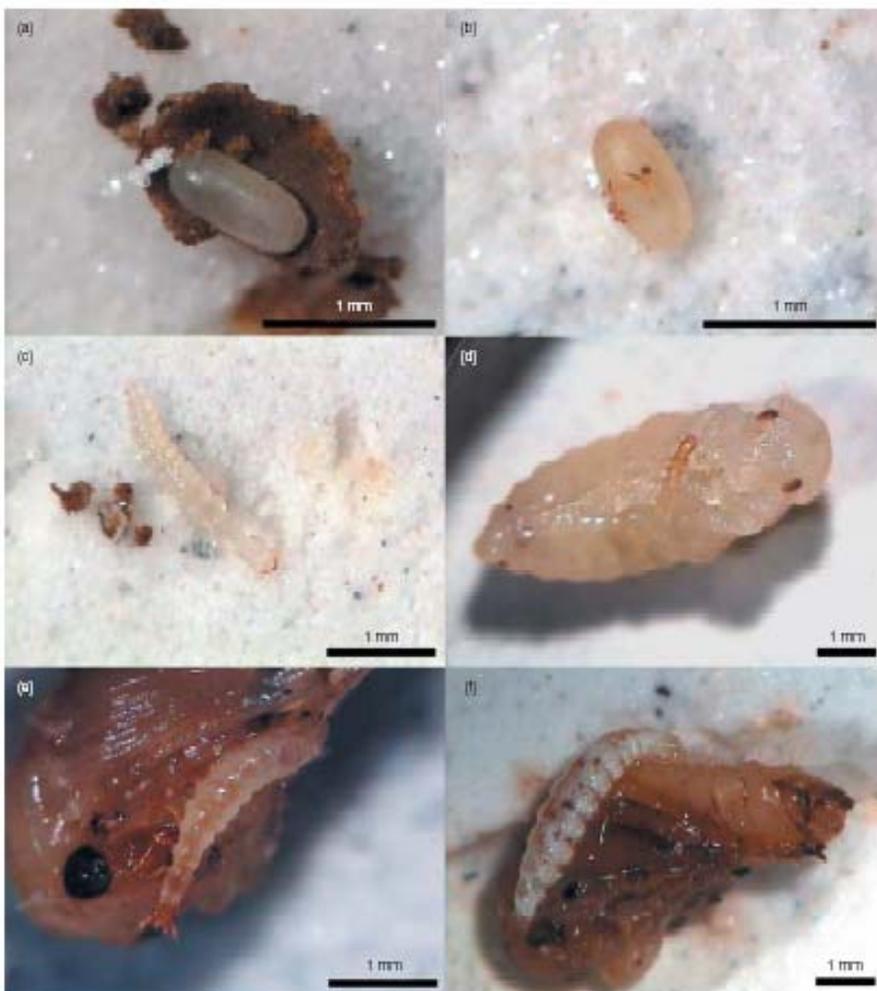


Fig. 1. Developmental stages of *Brachinus* species: (a) egg of *B. crepitans* in a mud cell; (b) egg of *B. crepitans* before eclosion, mandibles of the larva already visible; (c) first instar larva of *B. crepitans*; (d) first instar larva of *B. explodens* on the host; (e) first instar larva of *B. explodens* before ecdysis; (f) second instar larva of *B. crepitans* after ecdysis and in its typical feeding position.

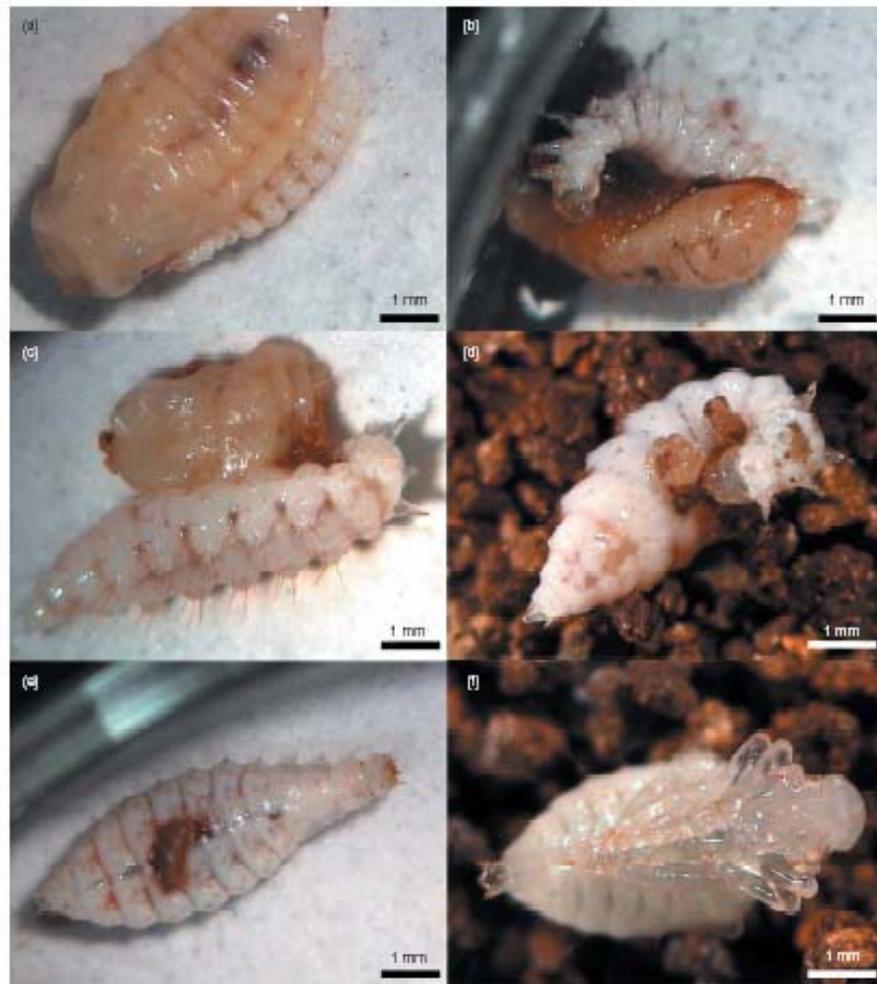


Fig. 2. Developmental stages of *Brachinus* species: (a) second instar of *B. crepitans* before ecdysis; (b) third instar larva of *B. crepitans* after ecdysis and before the beginning of the feeding phase; (c) third instar larva of *B. crepitans*, feeding; (d) third instar larva of *B. explodens*, end of the feeding phase, host almost consumed; (e) third instar larva of *B. explodens*, the prepupal phase; (f) newly formed pupa of *B. explodens*.

Table 4. Review of the species of the genus *Brachinus* with known hosts

<u><i>Brachinus</i> species</u>	<u>Host species</u>	<u>Host family</u>	<u>Reference</u>
<i>B. janthinipennis</i> Dejean	<i>Dineutus americanus</i>	Gyrinidae	Wickham (1893)
<i>B. cyanipennis</i> Say	<i>Dineutus discolor</i>	Gyrinidae	King (1919)
<i>B. pallidus</i> Erwin	<i>Berosus punctatissimus</i>	Hydrophilidae	Erwin (1967)
	<i>Tropisternus ellipticus</i>	Hydrophilidae	Erwin (1967)
<i>B. mexicanus</i> Dejean	<i>Berosus punctatissimus</i>	Hydrophilidae	Erwin (1967)
	<i>Tropisternus ellipticus</i>	Hydrophilidae	Erwin (1967)
	<i>Tropisternus lateralis</i>	Hydrophilidae	Juliano (1985)
<i>B. tenuicollis</i> Le Conte	<i>Hydrochara obtusata</i>	Hydrophilidae	James in Erwin (1970: 125)
<i>B. lateralis</i> Dejean	<i>Eretes sticticus</i>	Dytiscidae	Juliano (1984)
	<i>Tropisternus sublaevis</i>	Hydrophilidae	Juliano (1984)
	<i>Tropisternus lateralis</i>	Hydrophilidae	Juliano (1984)
	<i>Berosus</i> spp.	Hydrophilidae	Juliano (1984)
<i>B. javalinopsis</i> Erwin	<i>Eretes sticticus</i>	Dytiscidae	Juliano (1985)
<i>B. crepitans</i> (L.)	<i>Amara simulata</i>	Carabidae	Saska & Honek (2004)
<i>B. explodens</i> Duftschmid	<i>Amara aenea</i>	Carabidae	Saska & Honek (2004)

15 associations involving 9 *Brachinus* species; a fraction of the true total !

Lebia

over 450 species; cosmopolitan;
47 in North America

most speciose genus of Lebiini

all known *Lebia* larvae are ectoparasitoids of chrysomelids
but only four species' hosts documented

many other *Lebia* reported to be
associated with chrysomelids,
particularly Alticinae (flea beetles)

Lebia hosts

Lebia scapularis

Xanthogaleruca luteola

Silvestri 1904

Ulmus

Lebia grandis

Leptinotarsa decemlineata

Chaboussou 1939

Solanum

Lebia chlorocephala

Chrysolina varians

Lindroth 1954

Hypericum

Lebia viridis

Altica foliacea

Capogreco 1989

Oenothera

average rate of discovery: one relationship every 30 years !

Lebia scapularis
parasitoid of Elm leaf beetle,
Xanthogaleruca luteola (Müller)

F. SILVESTRI
CONTRIBUZIONI
ALLA CONOSCENZA
degli insetti dannosi e dei loro simbionti.

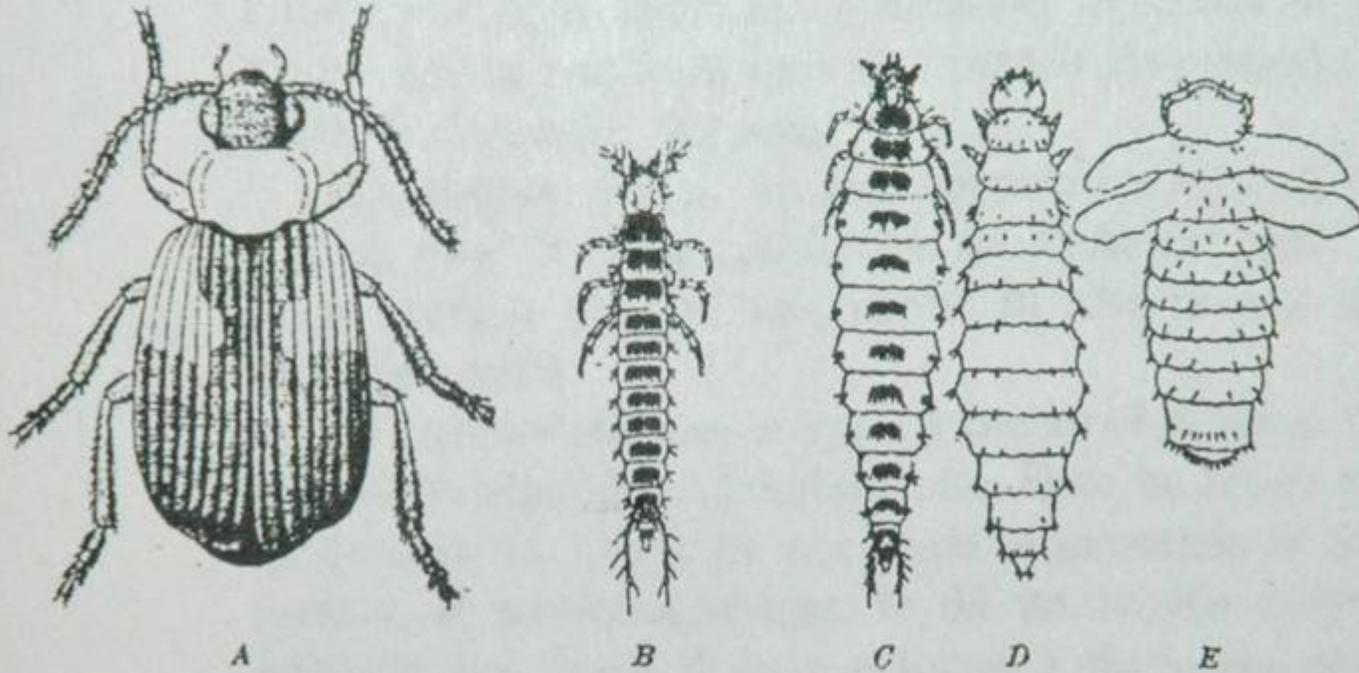
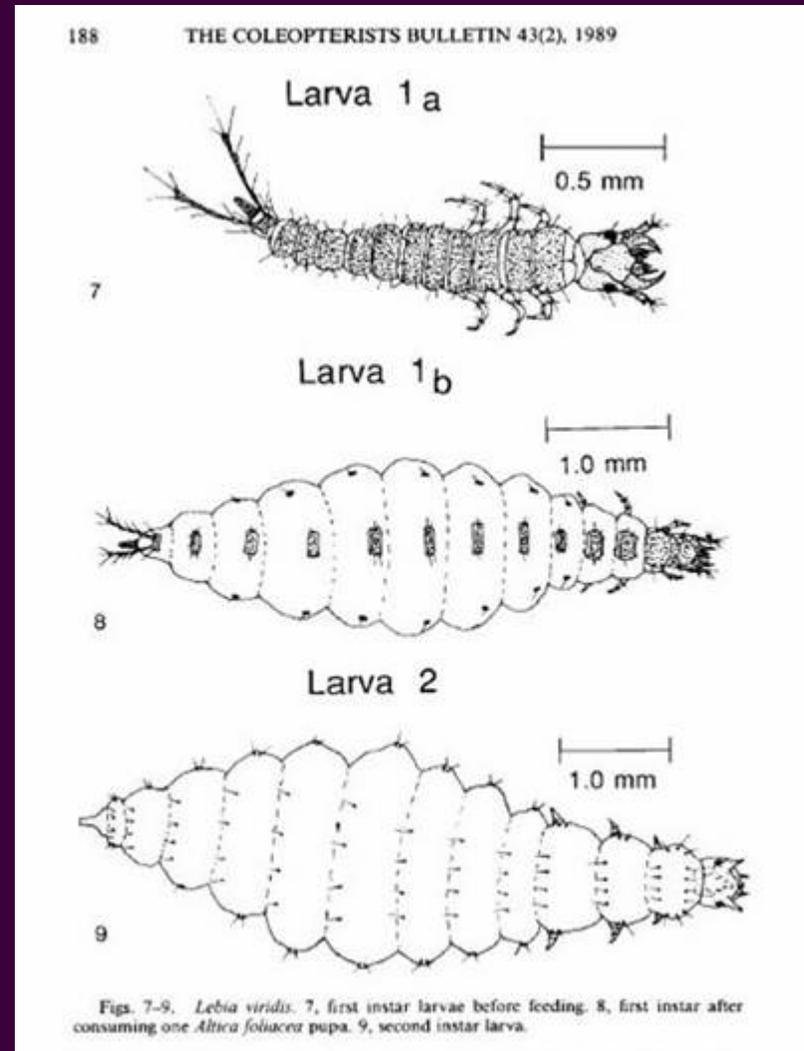


Fig. XIII.

A, adulto (ingrandito circa nove volte); B, larva del primo stadio (ingrandita circa quindici volte); C, larva del secondo stadio (ingrandita circa sei volte); D, larva del terzo stadio (ingrandita come la precedente); E, pupa (ingrandita circa sette volte).

Lebia viridis

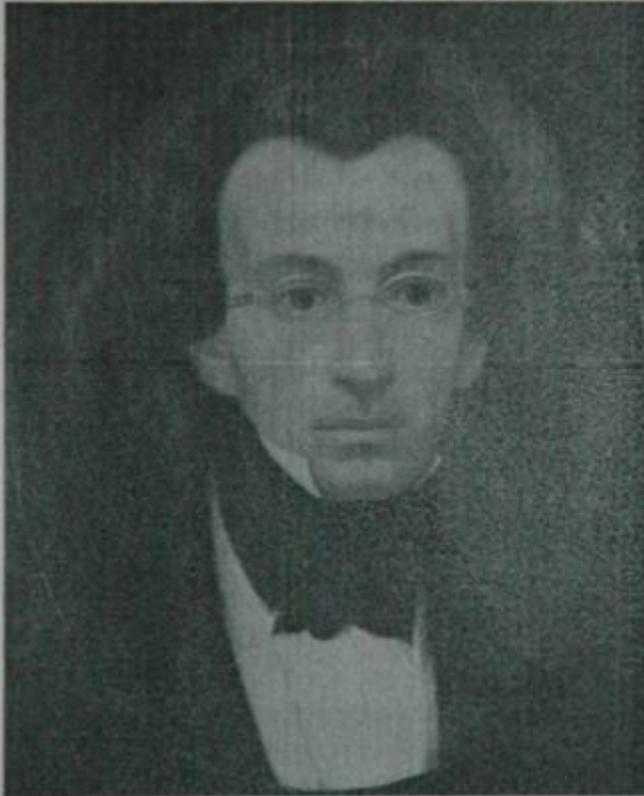
- parasitizes *Altica foliacea*, a flea beetle on evening primrose
- apparent mimicry of host (also noted for other *Lebia* and for *Lebistina*)
- females lay 4-5 single eggs per night; apparently univoltine
- first instar seeks out host pupa immediately after eclosing from egg
- larva crawls over pupa around pupal cell
- attaches laterally to first few abd. segments
- consumes entire pupa in 2-3 days
- then, inactive for 1-2 days, molts to 2nd instar
- 2nd does not feed, 4-5 days, molts to pupa
- pupal stage lasts 4-6 days
- *Lebia viridis* is associated with several other flea beetle hosts



Lebia grandis
(Coleoptera: Carabidae)



Lebia grandis Hentz 1830



Nicholas Marcellus Hentz (1797-1856)

LEBIA.

4. *L. grandis*. Ferruginous; elytra purple, venter piceous; thorax remarkably transverse, posterior angles sharp, nearly rectangular.

Length rather more than 9-20ths of an inch.

Inhabits North Carolina.

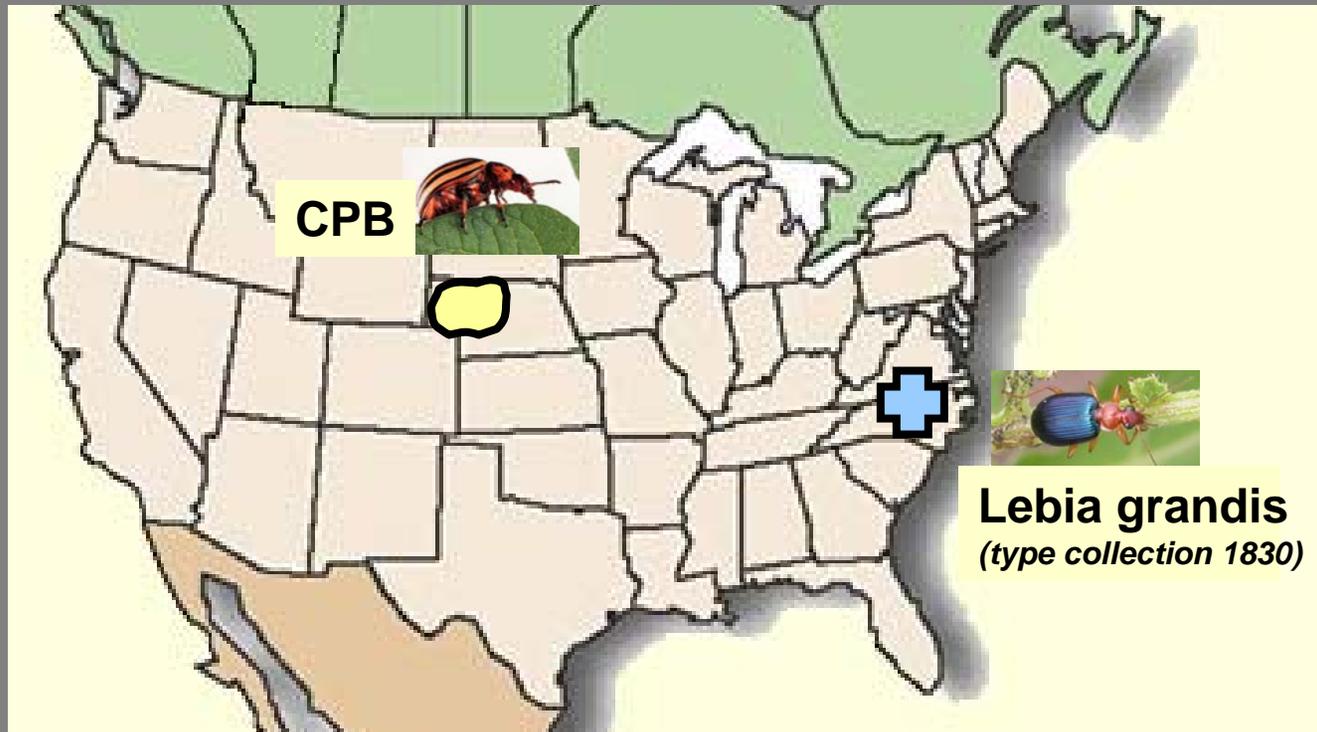
The remarkable size of this species will be sufficient to distinguish it from *L. atriventris*, Say, which it very much resembles; but it is nearly twice as large, being, I believe, enormous for this genus. The head is darker than the thorax, and the striæ of the elytra are deeper than in *L. atriventris*. I have never seen but two specimens, found at night, attracted by the light.

5. *L. borea*. Head dark green; disk of the thorax, tarsi, lower ends of the tibia, knees, and anterior thighs, piceous; elytra green, substriate; postpectus and venter ferruginous.

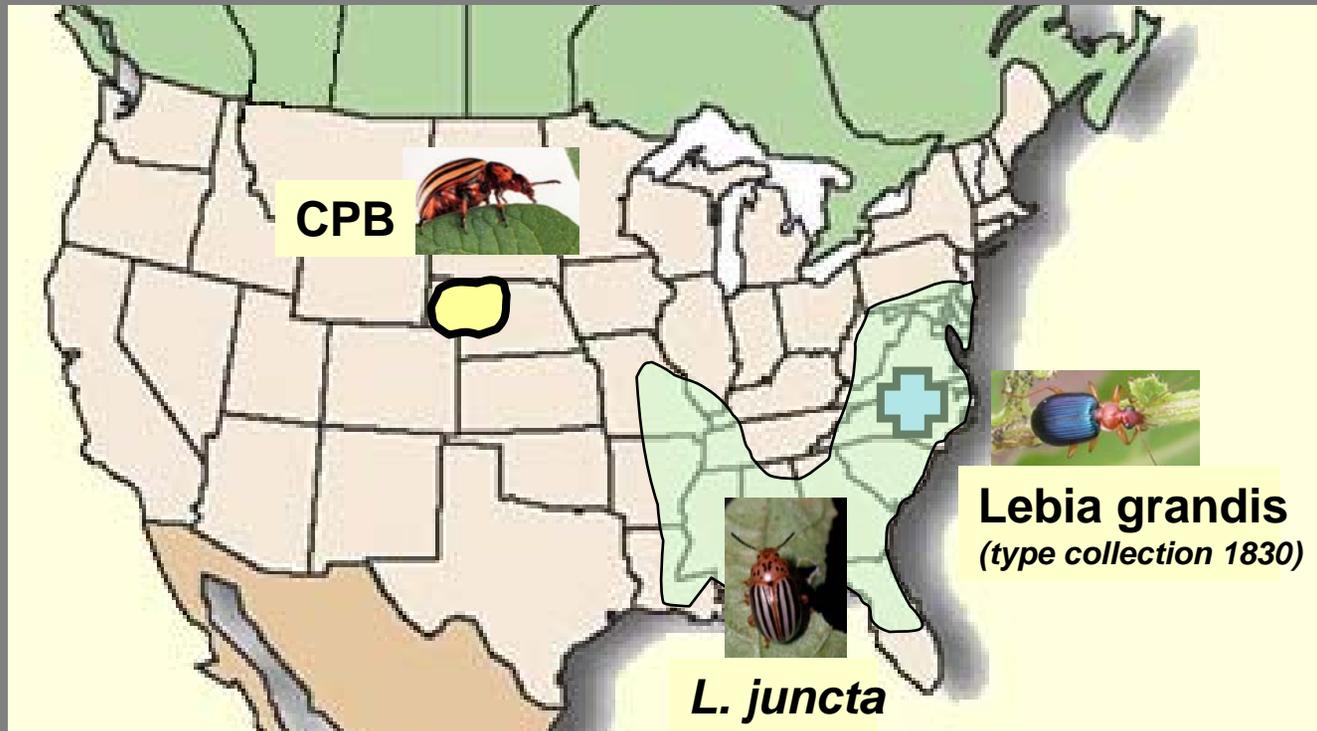
Length rather more than 5-20ths of an inch.

Inhabits Massachusetts.

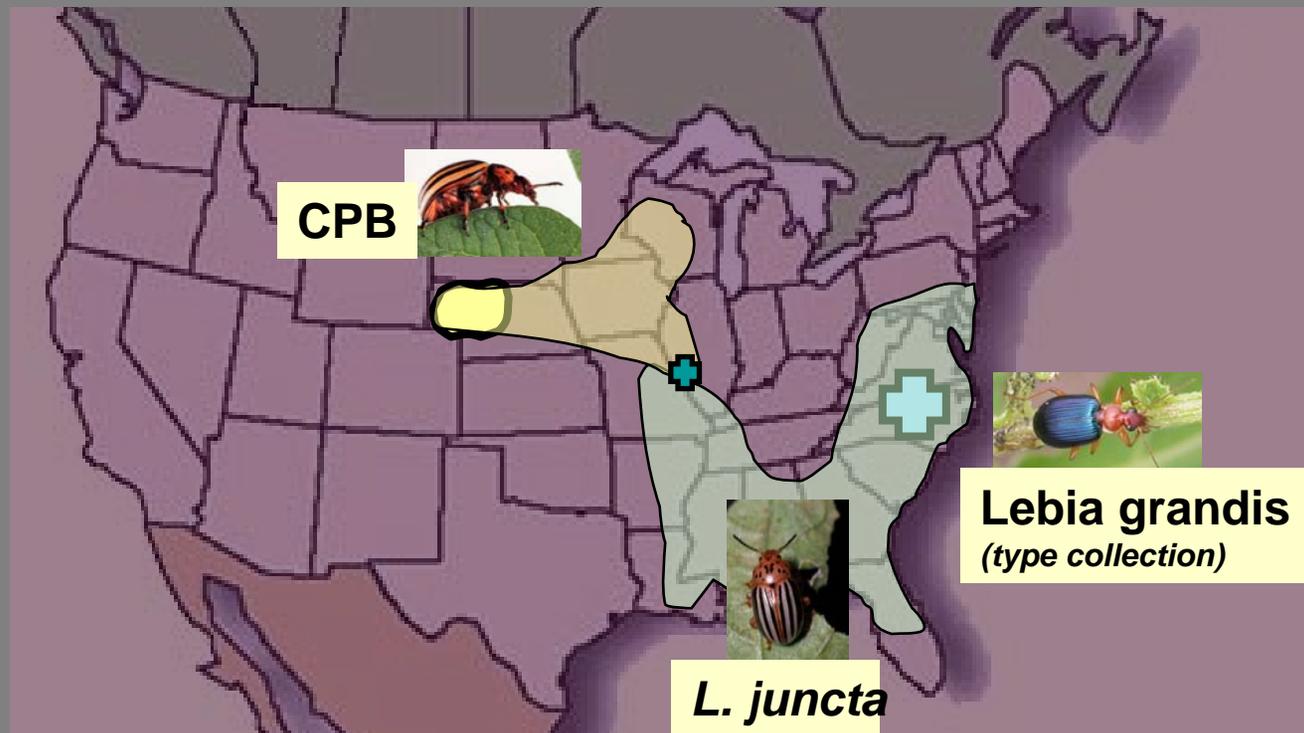
Recorded ranges of CPB and Lebia grandis in 1860 do not overlap. C.V. Riley did not mention *Lebia* in his exhaustive descriptions of natural enemies in the 1870s. CPB is apparently not the original host.



Type location for *Lebia grandis* does however **overlap** with range of *Leptinotarsa juncta*, native to southeastern U.S.A., which feeds on horsenettle, *Solanum carolinense*.



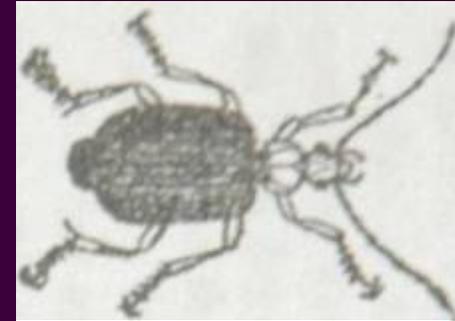
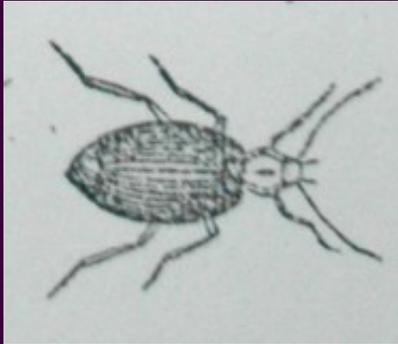
By 1868, the ranges of CPB and *L. juncta* overlap, due to rapid expansion of CPB toward the east. *Lebia grandis* is reported to U.S. Entomologist Townend Glover as abundantly feeding on CPB eggs and larvae in Pittsfield, Illinois: **the first report of the two species occurring together.**



By 1868, the ranges of CPB and *L. juncta* overlap, due to rapid expansion of CPB toward the east. *Lebia grandis* is reported to U.S. Entomologist Townend Glover as abundantly feeding on CPB eggs and larvae in Pittsfield, Illinois: *the first report of the two species occurring together*.



Lebia grandis preys on the Colorado potato beetle



the stripes with a single row of punctures, the legs also have a row of punctures in the middle of all the thighs. This insect (the *D. juncta*) I found and raised in South Carolina upon the horse nettle (*Solanum Carolinense*) and the Department has received several specimens from Montgomery, Alabama, where they fed upon potatoes and egg plants, being reported as especially injurious to the latter. The larvæ of the *decim lineata* are destroyed by a plant-bug, *Harpactor cinctus*, and other insects of the same order. Dr. Benjamin Norris, of Pittsfield, Illinois, found a species of ground beetle, *Lebia grandis*, feeding voraciously upon the larvæ in a potato field in that neighborhood. Hundreds of this comparatively rare insect were taken by him in the same locality, and always preying upon the grubs of the potato beetle, for the destruction of which many plans have been suggested. Mr. J.



NATURAL CHECKS INCREASING.

In many parts of the West this insect is being kept in due check by [Fig. 41.] its cannibal and parasitic enemies, which are still increasing. Thus we learn from many sources that in Iowa and Kansas it is not nearly so injurious as it formerly was, while in some parts of Illinois and Missouri it has also become less troublesome. Last year Mr. T. Glover published the fact that the Great *Lebia* (*Lebia grandis*, Hentz, Fig. 41) was found devouring its larvæ,* and though hitherto considered rare this *Lebia* has suddenly fallen upon it the present year in many parts of Missouri. During a recent trip along the Missouri Bottom we found this cannibal very abundant in some potato fields belonging to Mr. Wm. Coleman, where it was actively engaged in destroying both the eggs and larvæ of the Potato Beetles. The head, thorax and legs of this cannibal are yellowish-brown, in high contrast with its dark-blue wing-covers.

Glover T. 1868. Report of the Entomologist, pp. 58-76 in United States Commissioner of Agriculture, Agricultural Report for the year 1867.

Riley, C.V. 1869. Third Annual Report of the State Entomologist, St. Louis.



Lebia grandis
adult with snack

Lebia grandis travels to France

Colorado potato beetle reached east coast of North America in 1880; a threat to Europe and the reason for the first international plant quarantines; finally established to France in 1922

Soon thereafter, the Rockefeller Foundation funded a classical biological control effort which was assisted by Cornell University and USDA. Collections of *Podisus maculiventris* (Heteroptera Pentatomidae) and *Lebia grandis* were shipped to France for establishment against CPB.

Natural enemies travelled by boat and mortality was high. And then, there was the challenge to rear the carabid!

Lebia grandis discovered to be a parasitoid

CONTRIBUTION

À L'ÉTUDE BIOLOGIQUE DE *LEBIA GRANDIS* HENTZ.,

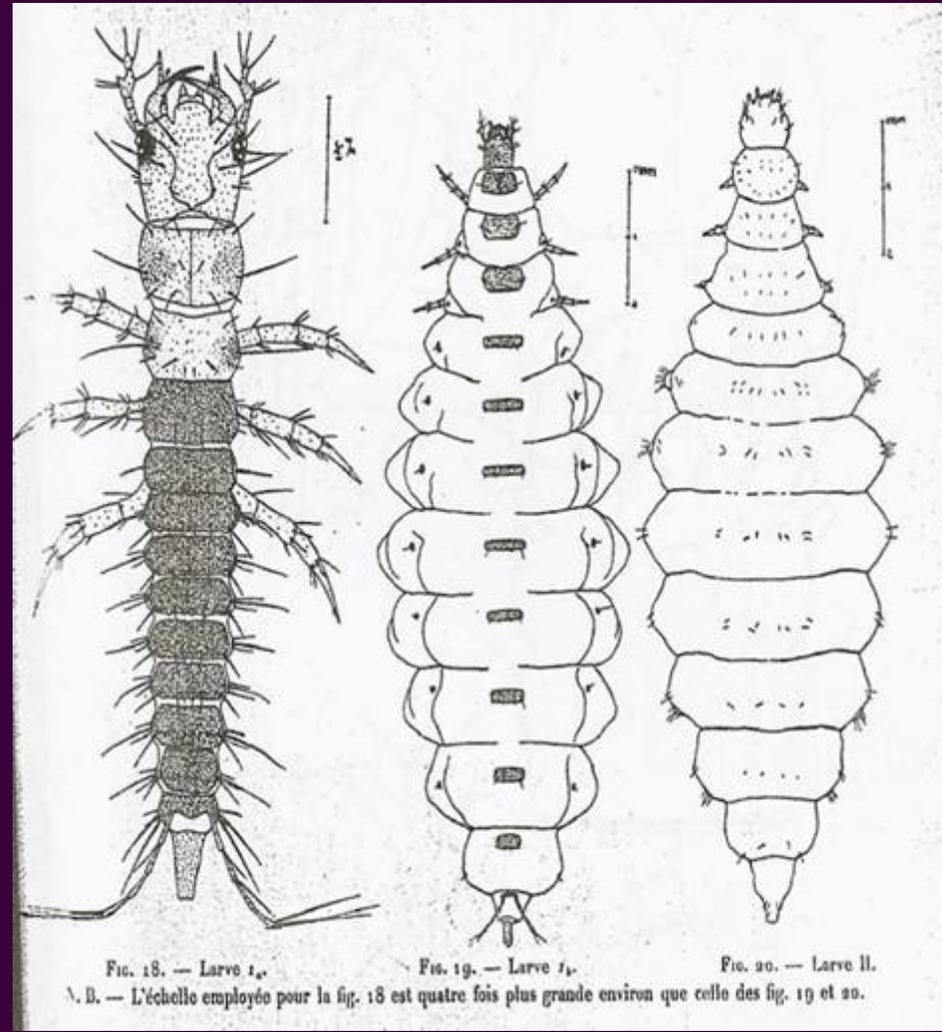
PRÉDATEUR AMÉRICAIN DU DORYPHORE,

par F. CHABOUSSOU,

Chef de travaux à la Station de Zoologie agricole du Sud-Ouest.

Adult is specialist predator on eggs
and all larval stages of CPB

Only recorded host is Colorado
potato beetle, *Leptinotarsa*
decemlineata (but more on this later)



Chaboussou, F. 1939. Contribution à l'étude biologique de *Lebia grandis* Hentz, prédateur américain du Doryphore. *Ann. Épiphyt. Phytogén. (N.S.)* 5:387-433.

1st-instar *Lebia grandis* larva
Seeks out the prepupa or pupa
underneath the soil, then
becomes an ectoparasitoid



CPB pepupae dig rapidly to their pupal site

Lebia 1st instar must follow soon after !





Lebia grandis, fed larva with host *Leptinotarsa decemlineata*

Pupa of *Lebia grandis*



Groden, E. 1989. Natural mortality of the Colorado potato beetle, *Leptinotarsa decemlineata* (Say) Ph.D. Dissertation Michigan State University, East Lansing.

MANUSCRIPT 2.

Biology and Seasonal Dynamics of *Lebia grandis* Hentz (Coleoptera; Carabidae), Predator and Parasitoid of the Colorado Potato Beetle, (Coleoptera: Chrysomellidae)

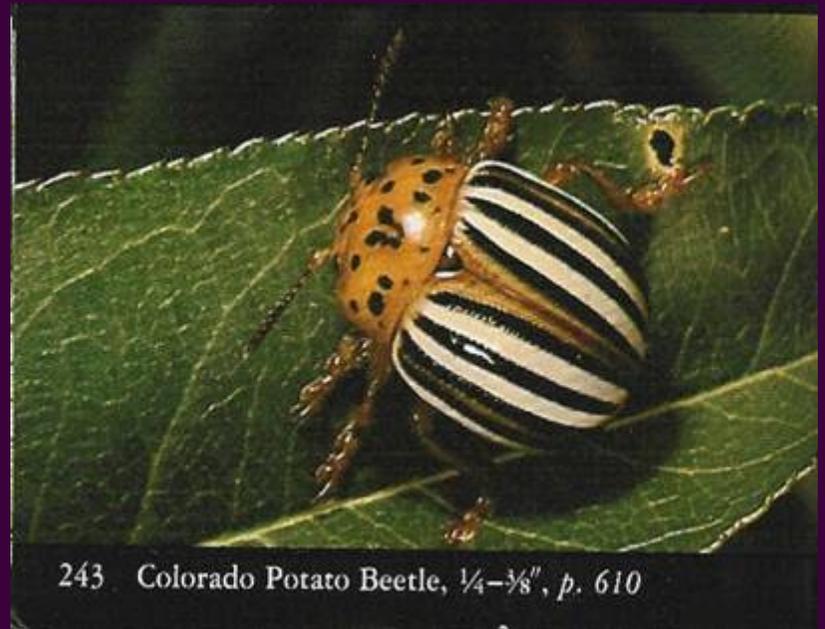
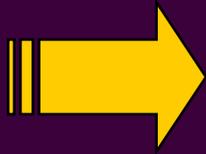
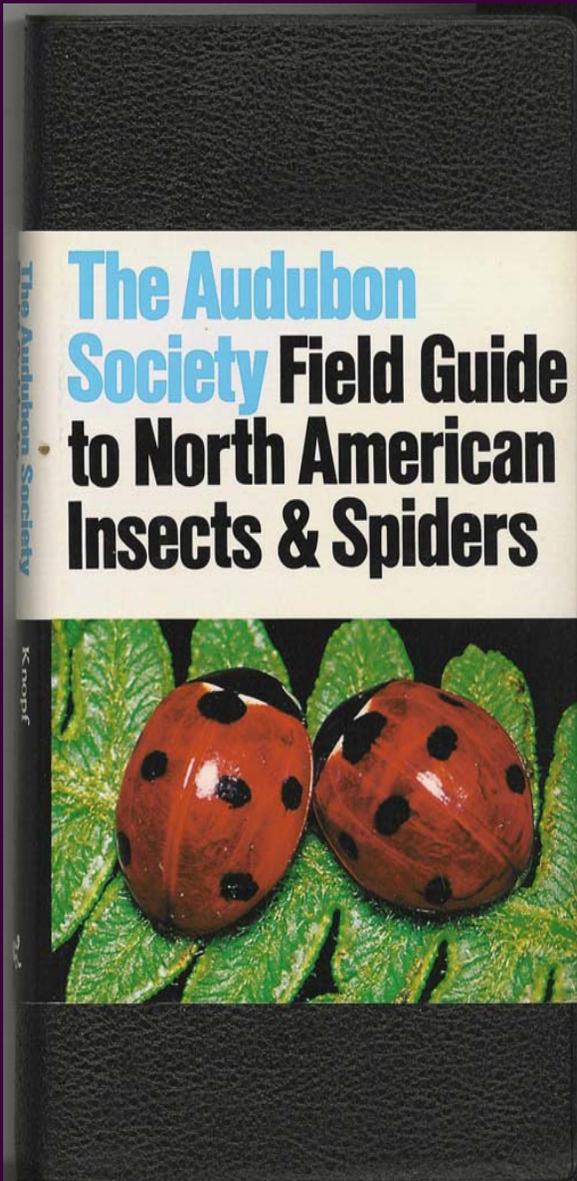
ABSTRACT - The biology and seasonal dynamics of the carabid beetle *Lebia grandis* Hentz were investigated in Rhode Island and Michigan, and its potential impact on Colorado potato beetle (CPB), *Leptinotarsa decemlineata* (Say) populations was evaluated. *L. grandis* fed on all immature stages of the CPB, and was found to feed over a wide range of temperatures. This predator appeared to be quite specific to the CPB, only feeding on aphids when CPB prey were absent. *L. grandis* consumed more CPB per day than the five other endemic natural enemies studied to date. Field cage studies

Leptinotarsa juncta



False potato beetle





243 Colorado Potato Beetle, $\frac{1}{4}$ – $\frac{3}{8}$ " , p. 610

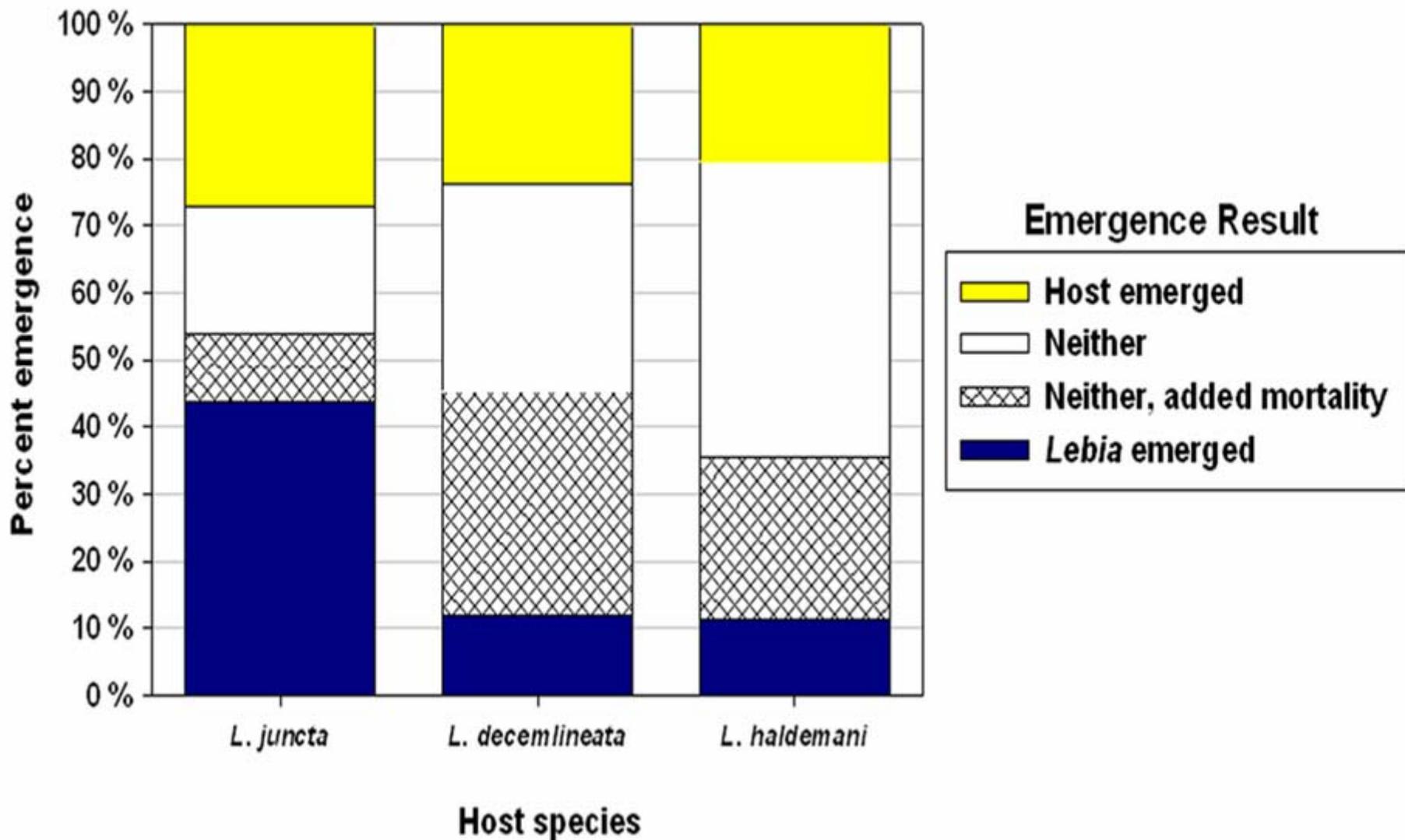
L. decemlineata

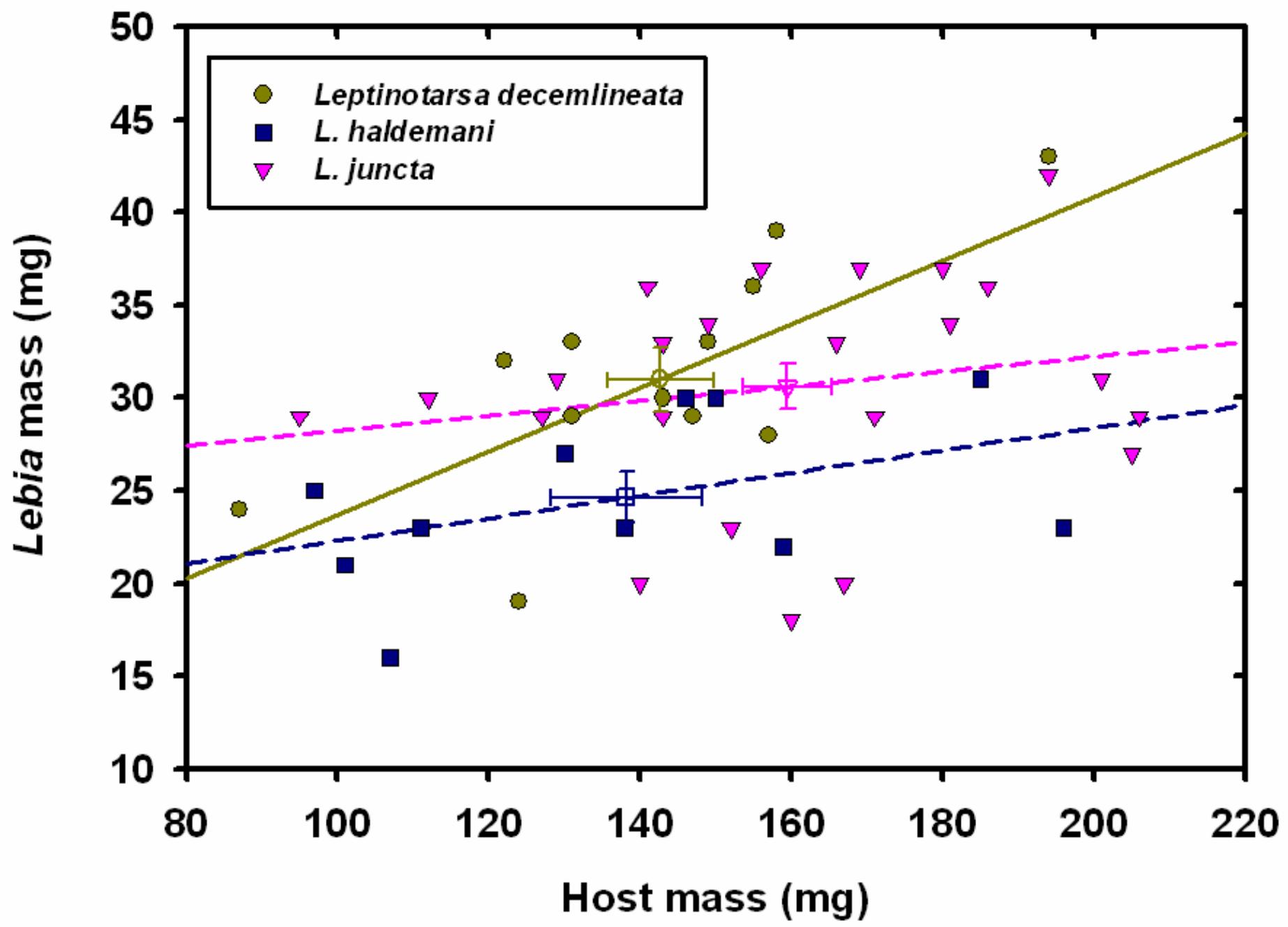
L. juncta

L. haldemani





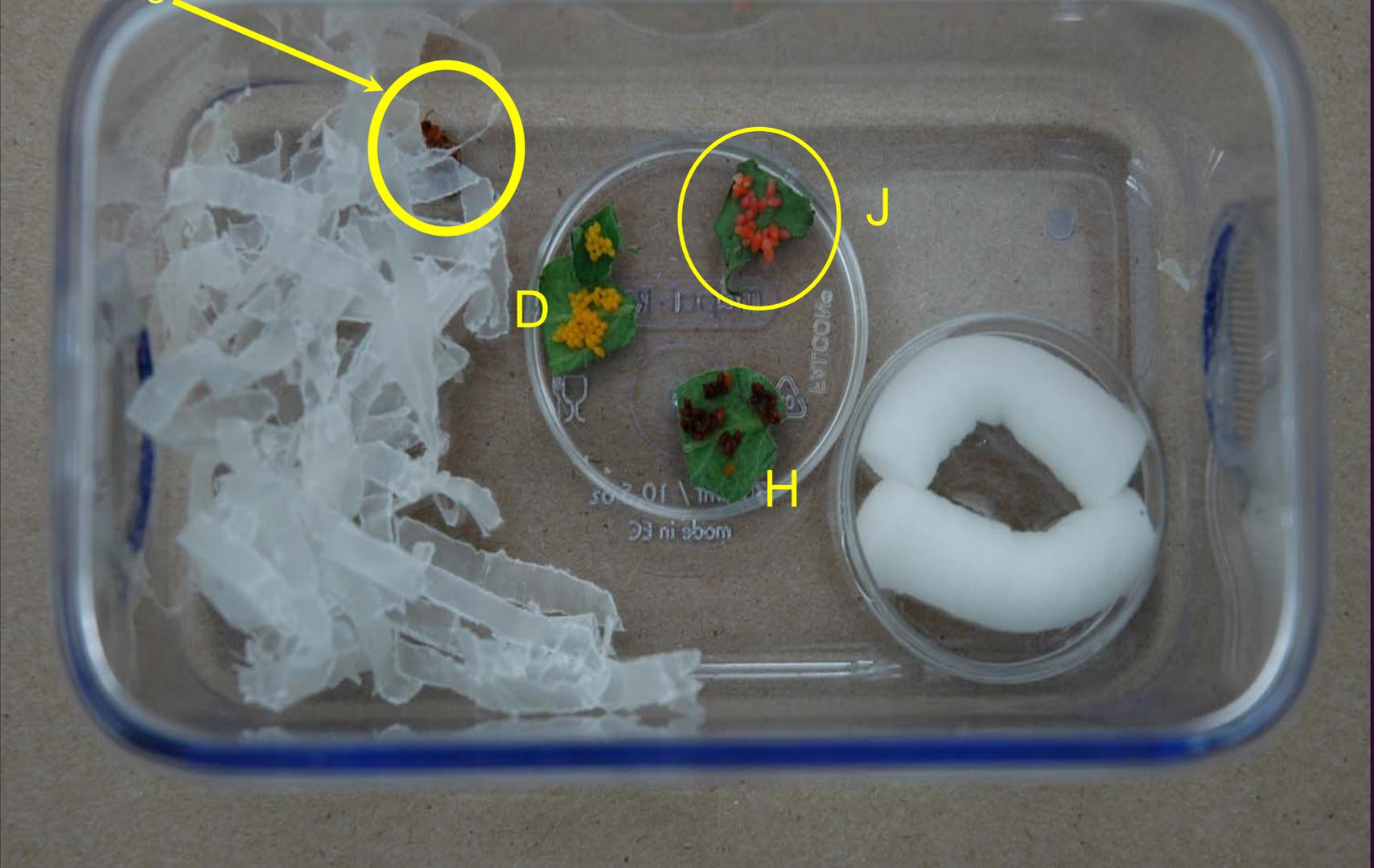




egg preference ?
yes, for *L. juncta*

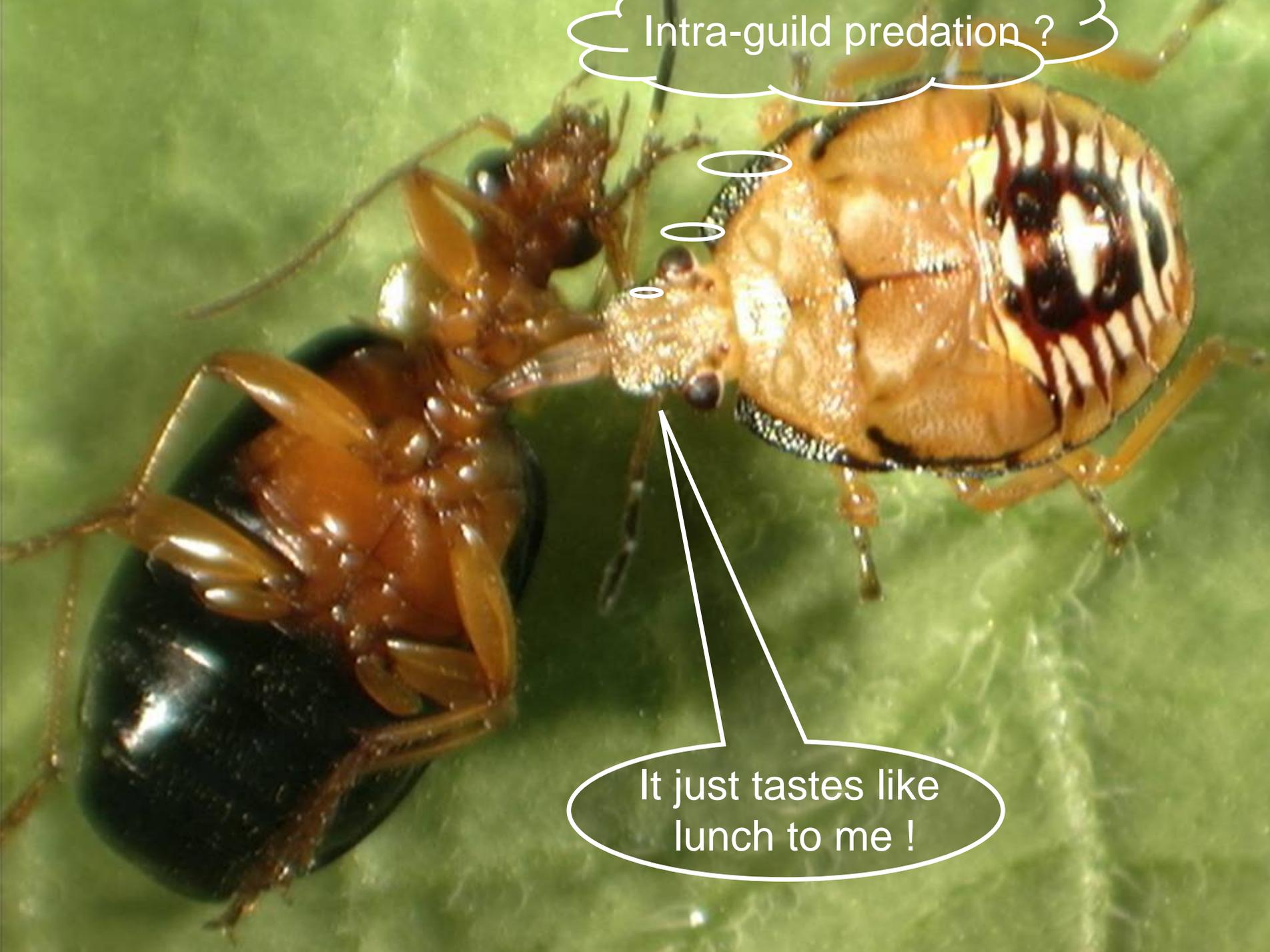
larval preference ?
none detected

adult *L. grandis*



Lebia grandis: the Odyssey

- Its only known host (CPB) was in all likelihood not its original host
- Its life cycle was unknown for more than 100 years, in spite of intense interest
- It had to travel to France before the parasitoid habit was discovered, yet, ironically, was never established there
- Nevertheless, it is the most voracious predator of eggs and larvae of Colorado potato beetle



Intra-guild predation ?

It just tastes like lunch to me !

Lebistina

Commiphora



Diamphidia



Lebistina



poison arrows



mammals



San Bushmen



Stories and open questions about parasitoid Carabidae

- arrow-poison of *Lebistina* and its host
 - leptinotarsin, a potent neurotoxin from *Leptinotarsa*
(Crosland et al. 2004)
 - aposematism/mimicry of many Lebiini
 - why is the pinnacle of defensive chemistry
(*Brachinus*) associated with the parasitoid habit?
-

More open questions about parasitoid Carabidae

- host relationships remain to be discovered for 99% of species !
 - implications of predator/parasitoid life cycle for population dynamics and interaction with host populations
 - implications of “double control” for effectiveness of natural enemy
 - role of plant chemistry in interaction of host and parasitoid
 - a raft of fascinating evolutionary questions
-

Acknowledgements

Funding: Cullman Fellowship (CSC)
USDA-ARS (DCW)

Photos: Terry Erwin, P. Saska & A. Honek, Iziko Museums

Advice and assistance with *Lebia grandis*:

Ellie Groden, Eric Riddick, Dan Rowley, Mike Athanas,
Jenn Curtis, Zsofia Szendrei



the end.